SEED SURFACE STRUCTURE IN THE GENUS *ZIERIA* SM. (RUTACEAE)

J. M. Powell and J. A. Armstrong

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ABSTRACT

Powell, J. M. and J. A. Armstrong (National Herbarium of New South Wales, Royal Botanic Gardens, Sydney, New South Wales, Australia 2000) 1980. Seed surface structure in the genus Zieria *Sm. (Rutaceae). Telopea 2 (1): 85–112.*—Seed surface structure of 119 samples representing 23 species of *Zieria* is examined, using the scanning electron microscope. Forty surface patterns are distinguished; thirty-eight are ridged, one is tuberculate and one colliculate-ribbed. The ridged surface patterns can be classified into three major groups and a number of subgroups on the basis of structural similarities. The taxonomic significance of the seed surface morphology is assessed by comparison with newly circumscribed taxonomic entities recognized on other morphological grounds by Armstrong. There is considerable concurrence between the seed data and the taxonomic entities but it is not universal. It is concluded that seed surface features provide a useful basis for distinguishing species and subspecies in only some instances within this genus. The close relationship indicated by general morphology within certain groups of taxa is supported by the seed data although, in general, phylogenetic conclusions cannot be based solely on seed surface structure.

INTRODUCTION

The genus *Zieria*, comprising some 27 species, is predominantly eastern Australian in distribution, extending from NE. Queensland to Tasmania and as far west as Kangaroo Island in South Australia; one species is endemic in New Caledonia. Bentham (1863) distinguished 10 species; since then a number of other taxa have been defined (Mueller 1875; Domin 1913; Maiden & Betche 1911, 1916: White 1932, 1942; Blakely 1941). The genus is being revised by Armstrong as part of a broader biosystematic study of the tribe Boronieae (Rutaceae).

Traditionally fruit and seed characters such as the fruit type (drupe, berry, capsule, samara), the number of cells in the fruit, the persistence or otherwise of the endocarp and the presence or absence of endosperm have been used in delimiting subfamilies and tribes within the Rutaceae (Bentham 1863; Engler 1931, 1964), but relatively little attention has been paid to seed surface structure.

Recent scanning electron microscope studies have provided detailed information on the surface patterns of small fruits and seeds (Heywood 1969, 1971) and have provided a firm base for the separation of closely related species in some genera e.g. *Carex* (Toivonen & Timonen 1976), *Cocculus* (Forman 1974), *Epilobium* (Seavey et al. 1977b), *Erica* (Huckerby et al. 1972), *Mentzelia* (Hill 1976) and *Scirpus* (Schuyler 1971), and for distinguishing subspecies and varieties within others, e.g. *Arenaria* (Echlin 1968) and *Cochlearia* (Godeau 1973a, b). Seed surface patterns are considered to be significant at higher taxonomic levels (sections, tribes, etc.) in *Cordylanthus* (Chuang & Heckard 1972), *Epilobium* (Skvortsov & Rusanovitch 1974; Seavey et al. 1977a) and *Sagina* (Crow 1979), and have been used for assessing relationships in *Scirpus* (Schuyler 1971), in *Mentzelia* (Hill 1976) and in the Melastomataceae (Whiffin & Tomb 1972). Much of the data available has been reviewed by Brisson & Peterson (1976).

An initial survey of *Zieria* seeds revealed various surface patterns and indicated a detailed study would be worthwhile. The aims of the study were, firstly, to describe in detail the seed surface patterns found in *Zieria* and to elucidate inter- and intra-specific variability, and secondly, to assess the usefulness of the seed data for taxonomic purposes.

TABLE 1

Voucher details of *Zieria* specimens studied

Sample Number	Taxon (Armstrong unpubl.)	Name used at NSW in 1975	Collector & No.
1	*Zieria arborescens* ssp. '*a*'	Z. arborescens Sims	Blake 23715 (BRI)
2	,,	,,	Close NSW 2770
3	,,	,,	Doney NSW 30526
4	,,	,,	French MEL 61977
5	,,	,,	Garden NSW 7311
6	,,	,,	Jacobs 51 (MEL)
7	,,	,,	Maiden NSW 2773
8	,,	,,	Merrall MEL 61989
9	*Zieria* sp. nov. '*F*'	Z. sp. aff. arborescens	Armstrong 115 (NSW)
10	,,	,,	Armstrong 744 (NSW)
11	,,	,,	Rodway NSW 19748
12	*Zieria aspalathoides* ssp. '*a*'	Z. aspalathoides A. Cunn. ex Benth.	Armstrong 999 (NSW)
13	,,	,,	Armstrong 1030 (NSW)
14	,,	,,	Biddulph 47 (BRI)
15	,,	,,	Clemens BRI 021762
16	,,	,,	Henderson 706 (BRI)
17	,,	,,	Henderson 1206 (BRI)
18	,,	,,	Streimann 631 (CBG)
19	,,	,,	Streimann 633 (CBG)
20	*Z. aspalathoides* ssp. '*b*'	,,	Boorman NSW 2725
21	,,	,,	Forsyth NSW 2734
22	,,	,,	Streimann 678 (CBG)
23	*Z. aspalathoides* ssp. '*c*'	,,	Gittins 919 (BRI)
24	,,	,,	Henderson 1098 (BRI)
25	*Zieria* sp. nov. '*A*'	Z. aspalathoides var. obovata C.T. White	Armstrong 1025 (NSW)
26	,,	,,	Fitzalan MEL 62269
27	,,	,,	Telford NQ 750 (CBG)
28	*Zieria* sp. nov. '*B*'	Z. aspalathoides var. nov. 'I'	Costin NSW 10525
29	*Zieria chevalieri*	Z. chevalieri Virot	McKee 5559 (NSW)
30	*Zieria fraseri* ssp. '*b*'	Z. compacta C. T. White	Armstrong 669 (NSW)
31	,,	,,	Jones CANB 189291
32	,,	,,	McKee 455 (MEL)
33	,,	,,	McKee NSW 22018
34	,,	,,	Pedley 1175 (BRI)
35	,,	,,	Streimann 575 (CBG)
36	*Zieria cytisoides* ssp. '*a*'	Z. cytisoides Sm.	Boorman NSW 2977
37	,,	,,	Constable 5168 (NSW)
38	,,	,,	Gittins 351 (BRI)
39	,,	,,	Rodway NSW 19727
40	,,	,,	Williamson MEL 62033
41	*Zieria cytisoides* ssp. '*b*'	,,	Burgess CBG 020402
42	,,	,,	Phillips CBG 005925
43	,,	,,	Phillips CBG 002887
44	,,	,,	*Anon.* MEL 62038
45	*Zieria furfuracea* ssp. '*a*'	Z. furfuracea R.Br. ex Benth.	Armstrong 551 (NSW)
46	,,	,,	Maiden NSW 2787
47	*Zieria furfuracea* ssp. '*b*'	,,	King s.n. (Coffs Harbour)
48	,,	,,	White BRI 021724
49	,,	,,	*Anon.* BRI 021725
50	*Zieria granulata*	Z. granulata (F.Muell.) C. Moore ex Benth. var. granulata	Boorman NSW 2855
51	,,	,,	Camfield NSW 2851
52	,,	,,	Camfield BRI 021617
53	*Zieria* sp. nov. '*C*'	Z. granulata var. adenodonta F.Muell.	*Anon.* MEL 62068
54	,,	,,	Carron MEL 62069
55	,,	,,	White 11876 (BRI)
56	*Zieria involucrata*	Z. involucrata R.Br. ex Benth.	Armstrong 804 (NSW)
57	,,	,,	Hamilton NSW 55952
58	*Zieria laevigata* ssp. '*a*'	Z. laevigata Sm.	Armstrong 750 (NSW)
59	,,	,,	Bäuerlen 126 (MEL)

TABLE 1—*continued*

Sample Number	Taxon (Armstrong unpubl.)	Name used at NSW in 1975	Collector & No.
60	*Zieria laevigata* ssp. '*a*'	Z. laevigata Sm.	Cheel NSW 2914
61	,,	,,	Garden NSW 4436
62	,,	,,	Garden NSW 4437
63	*Zieria fraseri* ssp. '*a*'	Z. laevigata var. fraseri (Hook.) Domin	Telford CBG 050542
64	*Zieria* sp. nov. '*D*'	Z. sp. aff. laevigata	Rupp NSW 13578
65	*Zieria laevigata* ssp. '*b*'	Z. laxiflora Domin	Armstrong 1160 (NSW)
66	,,	,,	Aston 89 (MEL)
67	,,	,,	Cheel NSW 2923
68	,,	,,	Clemens BRI 021624
69	,,	,,	Clemens BRI 021649
70	,,	,,	Clemens BRI 021650
71	,,	,,	Everist 7693 (CANB)
72	,,	,,	Hubbard 3905 (MEL)
73	,,	,,	Coveny 3808 (NSW)
74	,,	,,	White 6303 (BRI)
75	,,	,,	White 7105 (BRI)
76	*Zieria minutiflora* ssp. '*a*'	Z. minutiflora (F.Muell.) Domin	Dowling 17 (BRI)
77	,,	,,	Hunt BRI 118401
78	,,	,,	Moriarty 136 (BRI)
79	,,	,,	Simmonds BRI 111807
80	,,	,,	Telford 715 (CBG)
81	,,	,,	Hubbard 4116 (BRI)
82	*Zieria minutiflora* ssp. '*b*'	,,	Stevens QRS 000280
83	*Zieria murphyi*	Z. murphyi Blakely	Armstrong 212 (NSW)
84	,,	Z. pilosa var. canescens (R.Br.) Benth.	Caley s.n. (BM)
85	*Zieria obcordata*	Z. obcordata A.Cunn.	Ingram NSW 75929
86	*Zieria pilosa*	Z. pilosa Rudge	Armstrong 1257 (NSW)
87	,,	,,	Blakely NSW 2871
88	,,	,,	Briggs 3960 (NSW)
89	,,	,,	Camfield NSW 2884
90	,,	,,	Camfield NSW 2879
91	,,	,,	Fletcher NSW 2883
92	*Zieria robusta*	Z. robusta Maiden et Betche	Cambage 3180 (NSW)
93	*Zieria smithii* ssp. '*a*'	Z. smithii Andr.	Beckler MEL 62203
94	,,	,,	Boorman NSW 2560
95	,,	,,	Boorman NSW 2984
96	,,	,,	Cheel NSW 2979
97	,,	,,	Constable 5570 (NSW)
98	,,	,,	Constable NSW 56031
99	,,	,,	Durrington BRI 152495
100	,,	,,	Garden NSW 17247
101	,,	,,	Maiden NSW 3014
102	,,	,,	Phillips CBG 023871
103	,,	,,	Salasoo 2851 (NSW)
104	,,	,,	Scur 122 (NSW)
105	*Zieria smithii* ssp. '*b*'	,,	Armstrong 750 (NSW)
106	,,	,,	Armstrong 1020 (NSW)
107	,,	,,	Johnson MEL 62220
108	,,	,,	Tryon BRI 021697
109	,,	Z. sp. nov 'I'	Smith 3389 (BRI)
110	*Zieria* sp. nov. '*E*' ssp. '*a*'	Z. smithii Andr.	Everist 1169 (BRI)
111	*Zieria* sp. nov. '*E*' ssp. '*b*'	,,	Flecker QRS 000285
112	*Zieria* sp. nov. '*E*' ssp. '*c*'	,,	Armstrong 1032 (NSW)
113	,,	,,	Brass 20113 (BRI)
114	*Zieria veronicea*	Z. veronicea (F.Muell.) Benth.	Eichler 15176 (AD)
115	,,	,,	Eichler 18545 (AD)
116	,,	,,	Kraehenbuehl 1305 (AD)
117	,,	,,	Sutton MEL 62250
118	,,	,,	*Anon.* AD 96248108
119	*Zieria* sp. nov. '*G*'	Z. sp. nov. 'II'	Johnson MEL 62275

No seed samples were available of *Z. arborescens* ssp. '*b*' to ssp. '*f*', *Z. furfuracea* ssp. '*c*', *Z. smithii* ssp. '*c*', *Z.* sp. nov. '*H*' to '*K*'.

MATERIALS AND METHODS

Seeds used in the study were taken mainly from herbarium specimens deposited at the National Herbarium of New South Wales (NSW), and on loan from AD, BM, BRI, CANB, CBG, Coffs Harbour, MEL, and QRS. Some samples were taken from field collections and a few were obtained from living material grown in the research collection at the Royal Botanic Gardens, Sydney. Voucher specimens for these are held at NSW.

Since seed coat structure could be expected to differ at different stages of maturity, both immature and apparently mature seeds were selected for study. Samples were taken initially from the taxa recognized at NSW in 1975, i.e. prior to the start of the taxonomic revision. As the revision progressed, it became the taxonomic base for further sampling. The specimens studied are listed in Table 1 under both the earlier and more recent names (Armstrong, unpubl.).

Seed coat patterns were observed initially at 10–40x magnification using an Olympus stereomicroscope. For more detailed study seeds were mounted on specimen stubs with double-stick cellophane tape or with conductive silver paint. The specimens were then vapour-coated with 200–400 Å thickness of gold in a Polaron Coating Machine before being examined and photographed with a Cambridge Mark IV A Stereoscan Electron Microscope.*

All parts of the surface were studied in a detailed and systematic manner at magnifications between 50x and 5000x. Any variation of pattern from one part of the seed to another was noted. For comparative work, photographs were taken of the central area of the seed surface near the middle of the seed and occasionally also near the apex or base of the seed. Photomicrographs were standardized at 240x and 600x magnification for later study.

Because of the brittle seed coat it was impractical to prepare transverse sections for light microscopy and so scanning electron microscopy of transversely-fractured seeds was undertaken.

Surface pattern components

Most *Zieria* seed surfaces can be described in general terms such as rugulose, colliculate or tuberculate (Murley 1951) at magnifications up to c. 40x (Fig. 1A, B) but at much higher magnifications (100–600x or more) the surface pattern is too complex to portray in such terms.

To facilitate descriptions the following components of the patterns are described separately:

Ridges may be present or absent. When present they may be well-developed and either prominent and crested (i.e. rising high above the inner-ridge surface but sloping to it, Fig. 2A, B), prominent and erect (i.e. rising vertically above the ridge surface, Fig. 2D), or not prominent (i.e. not well-developed, Fig. 2C). The ridges may be continuous over most of the seed length (2000–4500 μm) or short, only 30–40 μm in length in some instances; they may have few or many branches and cross-ridges (Fig. 2F, G). In structure they may appear single (Fig. 3A, B) or be clearly double (Fig. 3C–F). Ridge width varies greatly from very narrow (less than 7 μm across) to extremely broad (greater than 28 μm across) and the distance between ridges varies greatly also, in some instances being less than 20 μm, in others over 100 μm. Individual *ridge units* (Fig. 3A–F) may be distinct or indistinct, rectangular or oval in shape and have a smooth or patterned surface.

* Located at the Electron Microscope Unit, School of Biological Sciences, University of New South Wales.

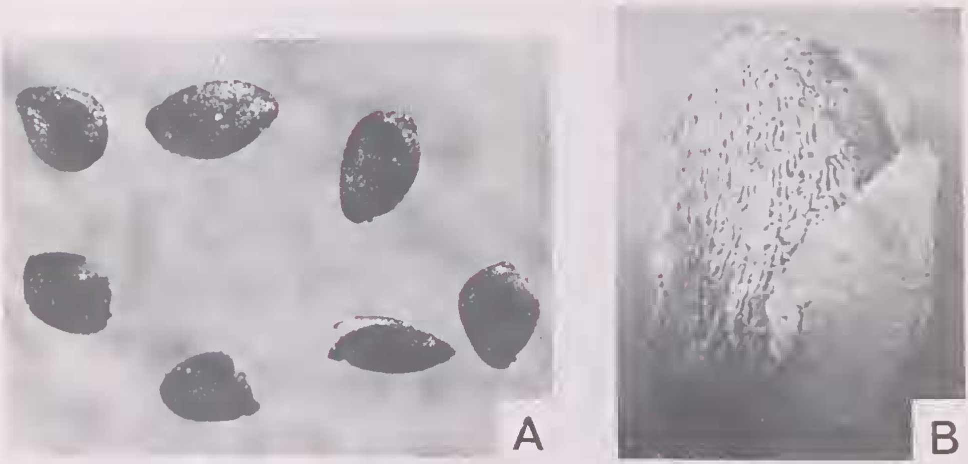

Fig. 1. *Zieria* seeds. A. Variation in size and shape, x 7. B. Scanning electron micrograph of whole seed with elaiosome attached, x 20.

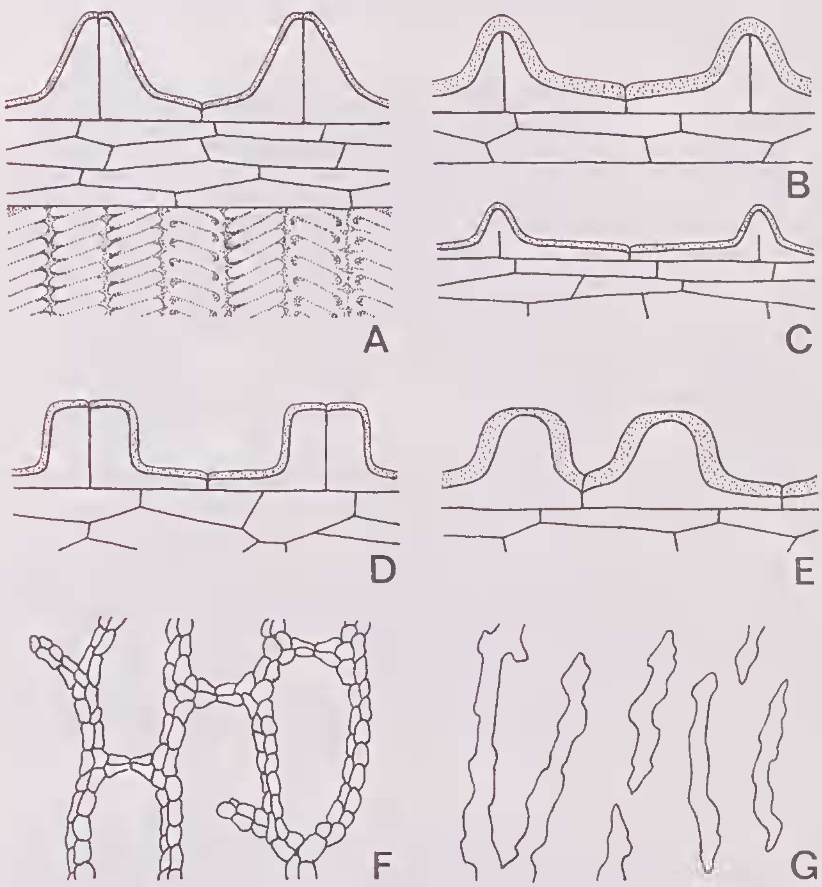

Fig. 2. Seed structure in *Zieria*. A–D. *Transverse sections showing ridge types*. A, B. Well-developed, prominent, crested. C. Not well-developed. D. Well-developed, prominent, erect. E. *Transverse section* of tuberculate seed. F–G. *Surface features of ridges*. F. Ridges long, with many branches and cross-ridges. G. Ridges short, with few branches and no cross-ridges.

An *inter-ridge pattern* (Fig. 3G–I) may be present or absent; if present it may be distinct or indistinct. The inter-ridge units can be described in terms of their shape and size, namely long-rectangular (usually 35–45 μm long, 15–18 μm wide; Fig. 3G), rectangular (usually 25–35 μm long, 15–18 μm wide), short rectangular or almost square (usually 15–25 μm across), triangular (18–24 μm per side; Fig. 3H) and oval to round (15–25 μm across; Fig. 3*I*). The units may be arranged somewhat irregularly between the ridges or aligned in 2–5 transverse rows. The *inter-ridge surface* may be ribbed (with the margins of the long-rectangular or rectangular units sunken, the centres raised; Fig. 3J), colliculate (with the margins of the short rectangular, triangular or oval units sunken, the centres raised; Fig. 3K), undulate (with the margins of the units—usually oval, triangular or short-rectangular—raised, the centres sunken; Fig. 3L), flat, concave or rugose. The inter-ridge *unit surface* may be smooth or patterned in various ways; it may be weakly striate or flecked (Fig. 3M), strongly striate (Fig. 3J), finely scabrate (Fig. 3K), coarsely scabrate (Fig. 3N), rugose, or coarsely scabrate-striate (Fig. 3*O*). *Wax* may be present or absent on the surface between the ridges; if present it may be sparse, common or abundant, persistent or non-persistent. The wax may appear as large flakes (Fig. 3P), crystals (Fig. 3Q), compact flocs or powdery flocs (Fig. 3R).

Slight changes in surface pattern often occur towards the edges of the seeds; the size of the units may vary somewhat and the regularity of the pattern decreases. The descriptions cover the range of pattern present over the major portion of the dorsal and ventral surfaces.

OBSERVATIONS AND DISCUSSION

Forty seed surface patterns can be described from the 119 samples of seed available for study; these are illustrated in Figures 4–13. Thirty eight types are ridged; within these considerable diversity in detailed pattern can be discerned with the scanning electron microscope and an attempt has been made to analyse this pattern both quantitatively and qualitatively (Tables 2–5). The other two types are very distinct: one is colliculate-ribbed (pattern 39, Fig. 13E, F), the other tuberculate (pattern 40, Fig. 13G, H). Detailed descriptions of mature and immature seed surface patterns, together with all photographs, are held at NSW.

Ridged surface patterns

(1) Criteria used for comparisons

For comparative purposes the most useful criteria are ridge width and length, spacing of ridges and the frequency of branches and cross-ridges since these can be measured directly or readily assessed qualitatively. In mature seeds the surface sculpture appears to be formed from the upper layer of 3–4 transverse cell layers which overlay a broad, hard, columnar cell layer (Fig. 2A–D). The ridges comprise vertical projections of parts of two adjoining cells. Ridge heights vary from 10 μm (sample 80, pattern 13) to 60 μm (sample 61, pattern 2) with from 30% (sample 93, pattern 22) to 80% (sample 61, pattern 2) of the total length of the cell upright. The cutin covering the cells varies somewhat in thickness and in sample 56 (pattern 15) obscures the underlying double structure of the ridge (Fig. 2B). In the tuberculate-patterned seed (sample 86, pattern 40) each tubercle is a single cell covered by very thick cutin (Fig. 2E).

The inter-ridge pattern in most cases is constant but in some varies from one part of the seed to another, e.g. in seed samples 21 (pattern 9), 64 (pattern 7) and 73 (pattern 8) the inter-ridge surface is ribbed in some areas but flat in others. In sample 93 (pattern 22) and sample 100 (pattern 24) the inter-ridge pattern is more ribbed towards the side of the seed and in sample 98 (pattern 26) the ridges are very poorly developed in parts. Assessment of inter-ridge pattern development, structure, and surface is relatively easy in seeds that lack wax; in those with wax, assessment of these criteria depends upon finding wax-free areas.

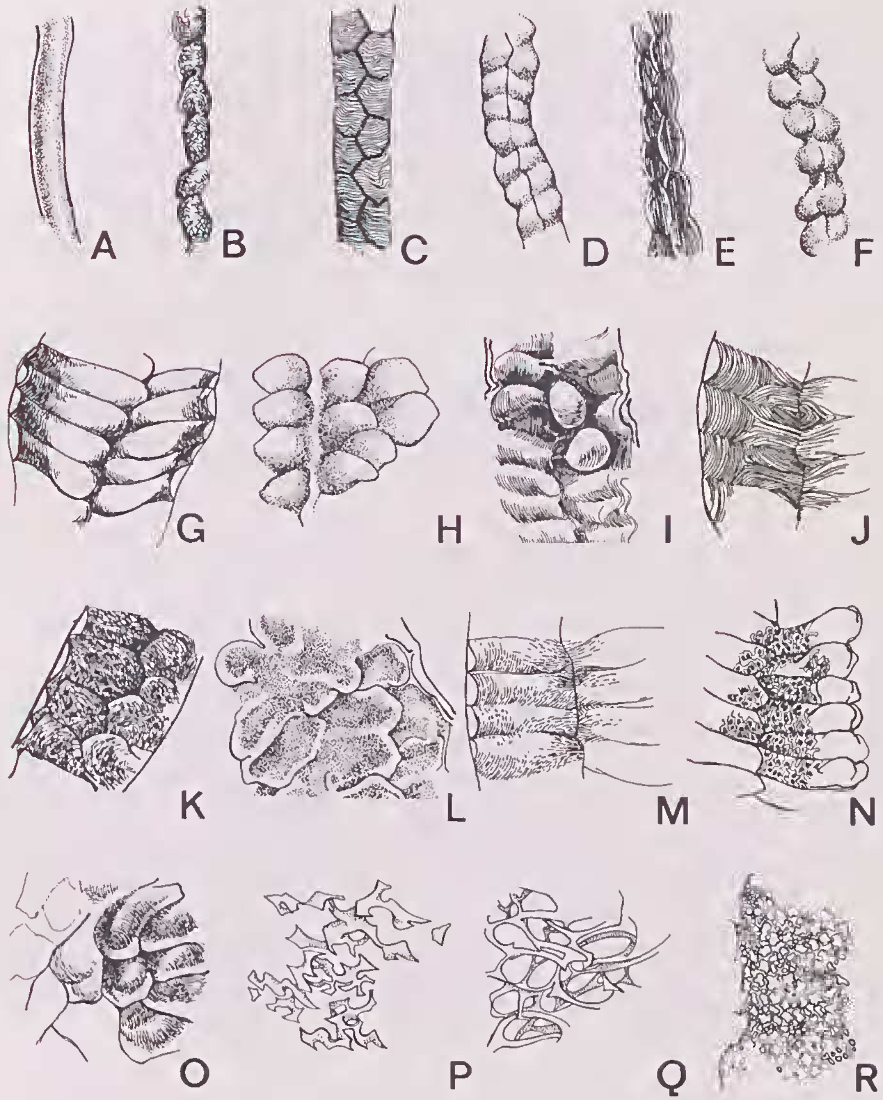

Fig. 3. Surface pattern components of *Zieria* seeds. A. *Ridge units* indistinct, smooth-surfaced. B–F. *Ridge units* distinct. B. Patterned-surface. C. Angular, strongly patterned. D. Oval, smooth-surfaced. E. Oval, chained, with concave surface. F. Pear-shaped, chained, smooth-surfaced. G–I. *Inter-ridge units*. G. Long-rectangular. H. Triangular. I. Oval to round. J–O. *Inter-ridge surface structure and unit surface texture*. J. Ribbed, strongly striate. K. Colliculate, finely scabrate. L. Undulate, smooth. M. Ribbed, weakly striate or flecked. N. Ribbed, coarsely scabrate. O. Colliculate, scabrate-striate. P–R. *Wax structure*. P. Flakes. Q. Crystals. R. Flocs.

Presence or absence of wax is readily observed and can be considered as an important distinguishing attribute. In one case, however, (sample 37, pattern 18) the wax is non-persistent, being found only at the immature stage, while in another, seeds with identical surface patterns may or may not have wax (samples 80, 82, pattern 13). Differences in wax structure are usually clear, but in a few cases it is difficult to distinguish between fine crystalline wax and wax flocs. It seems likely that the appearance of the wax may change somewhat with increasing maturity of the seed. The abundance of wax varies with the stage of maturity and hence this particular attribute is of limited comparative value.

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(2) Sampling problems

Out of the 38 ridged seed surface patterns distinguished 11 are represented by a single sample only and a further 8 by two samples only (Tables 2–5). The study of further material (when available) could lead to an overlap in the range of variation in some cases, e.g. pattern 23 (Fig. 9E, F) with pattern 24 (Fig. 10G, H), 4 with 5 (Fig. 4G, H; Fig. 5A, B), and pattern 7 (Fig. 5E, F) with pattern 8 (Fig. 5G, H). In other cases the distinctiveness of the surface pattern suggests that overlap with other patterns is unlikely: within this category are patterns 1, 3, 10, 11, 15, 17, 27, 30, 31, 32, 33, 34, 35, 36 and 37 (Figs. 4, 7, 8, 10–13). The remaining 19 patterns are represented by 3–9 samples each and appear to be constant.

(3) Classification of patterns

The ridged surface patterns can be classified into 3 major groups and a number of subgroups on the basis of structural similarities (Tables 2–5)*. The degree to which these reflect relationship or parallel evolution is unknown at present since there is no information available about the effects of selection pressures upon seed surface structure.

Group I: Patterns 1–13 (Table 2, Figs. 4–7) form a group characterized by prominent, broad ridges which are clearly double and usually smooth-surfaced; wax is always present. Subgroup A (patterns 1–3, Fig. 4) show a strongly ribbed inter-ridge surface, subgroup B (patterns 4–9, Figs. 4–6) show some ribbing but also have flat areas present between the ridges, and subgroup C (patterns 10–13, Figs. 6–7) are usually flat between the ridges.

Group II: This group, comprising patterns 14–26 (Table 3, Figs. 7–10) is rather less coherent than Group I but in all cases the mature seeds lack wax. Most types within this group have long, prominent, crested ridges which are smooth-surfaced but rather narrow. Subgroup A (patterns 14–18, Figs. 7–8) has ridges 16–25 μm wide and a strongly ribbed inter-ridge surface except when cross-ridges are abundant; the inter-ridge surface then appears concave (pattern 18, Fig. 8C, D). Subgroup B (patterns 19–22, Figs. 8–9) has much narrower ridges (6–8 μm wide) which appear to be single in structure, and a ribbed or colliculate (pattern 22, Fig. 9C, D) inter-ridge surface. Subgroup C (patterns 23 and 24, Figs. 9C, D; E, F) is very similar to Subgroup B but cross-ridges are abundant and hence the inter-ridge surface appears concave, flat or undulate. The types in Subgroup D (patterns 25 and 26, Fig. 10A, B; C, D) lack cross-ridges and have a flat inter-ridge surface.

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* **Key to Attributes in Tables 2–5**

Ridge development: 1 = not prominent, 2 = prominent and crested, 3 = prominent and erect.

Ridges long = +, short = –

Ridges smooth = +, patterned = –

Ridges single = +, double = –

Ridges with many branches = +, with few branches = –

Ridge units distinct = +, indistinct = –

Cross-ridge frequency: 0 = absent, 1 = few, 2 = many.

Inter-ridge development pattern: 0 = absent, 1 = indistinct, 2 = distinct.

Inter-ridge pattern structure: 1 = long-rectangular units, 2 = rectangular units, 3 = short-rectangular units, 4 = triangular units, 5 = oval to round units, ( ) = uncommon.

Inter-ridge surface texture: 1 = ribbed, 2 = colliculate, 3 = undulate, 4 = flat, 5 = concave, 6 = rugose.

Unit surface texture: 1 = smooth, 2 = flecked (weakly striate), 3 = striate, 4 = finely scabrate, 5 = coarsely scabrate, 6 = rugose.

Wax development: 0 = absent, 1 = non-persistent, 2 = persistent.

Wax abundance: 1 = sparse, 2 = common, 3 = abundant.

Wax structure: 1 = crystals, 2 = compact flocs, 3 = powdery flocs, 4 = flakes.

TABLE 2

Seed surface structure of ridged *Zieria* seeds: Group I

Attribute* — Subgroup	A			B						C			
Pattern No.	1	2	3	4	5	6	7	8	9	10	11	12	13
Ridge development	2	2	2	3	3	3	3	3	3	3	3	3	3
,, spacing (μm)	60–105	60–85	35–45	35–55	50–120	30–60	45–90	50–75	42–60	30–50	50–85	40–65	50–70
,, width (μm)	25–30	25–30	21–24	16–20	18–28	18–28	18–20	24–30	24–30	14–20	21–27	15–21	15–24
Ridges long	+	+	+	+	+	+	–	–	+	+	–	+	+
,, smooth	+	+	+	+	+	+, –	+	+	+	+	+, –	+	+
,, single	–	–	–	–	–	–	–	–	–	–	–	–	–
,, with many branches	–	–	–	–	+	–	–	–	–	–	–	+	–
Ridge units distinct	+	+	+	+	+, –	+	–	+	+	+	+	–	+
,, unit length (μm)	21–28	18–20	15–18	12–16	15–20	14–18	15–20	18–24	18–21	21–24	18–21	18–21	20–24
,, ,, width (μm)	14–18	15–20	10–12	8–10	9–14	10–14	8–12	12–15	15–18	12–15	12–18	12–15	12–14
Cross-ridge frequency	0	1	1	0	2	1	0	0	1	1	0	1	1
Inter-ridge pattern development	2	2	2	0, 1	0, 2	2, 1	2	2	0,1	0, 2	0	1	2
,, structure	1, (5)	1	3	3	1, (5)	2, 3, (5)	1, 5	1, 5	2	2, 3, (5)	–	3, 5	3, 4, 5
Rectangular unit length (μm)	45–55	35–45	18–21	14–18	50–60	30–35	40–50	35–45	30–40	25–30	–	18–20	18–22
,, ,, width (μm)	25–30	15–25	12–15	12–18	10–14	14–17	18–22	18–21	18–24	15–20	–	20–22	16–20
Oval unit diameter (μm)	15–20	–	–	–	15–20	14	20–30	24–27	–	15–20	–	15–20	26–30
Triangular unit dimensions (μm)	–	–	–	–	–	–	–	–	–	–	–	–	18–20
Inter-ridge surface	1	1	1	1, 4	1, 4	1, 4	1, 4	1, 4	1, 4	4	4	4	3, 4
Unit surface texture	5	1	1	1	1, 4	1	1	1	1	1	1	1	1
Wax development	2	2	2	2	2	2	2	2	2	2	2	2	0, 2
Wax abundance	2	1	2	1, 2	2, 3	2, 3	3	3	3	3	3	1	1
Wax structure	1	1	2	1, 3	(1), 3	1	3	1, (2)	1	1	1	1	3
Sample Numbers	63	58, 59, 60, 61, 62	33	29	30, 31, 32, 34, 35	12, 15, 16, 18, 19, 23, 24	64	65, 66, 67, 70, 71, 72, 73, 74, 75	20, 21, 22	17	68, 69	25, 26, 27	77, 78, 80, 81, 82

* For key to attributes see p. 92

TABLE 3

Seed surface structure of ridged *Zieria* seeds: Group II

Attribute* — Subgroup	A					B				C		D	
Pattern No.	14	15	16	17	18	19	20	21	22	23	24	25	26
Ridge development	2	2	2	2	3	2	2	1	1	2	2	2	3
,, spacing (µm)	50–70	60–80	35–45	30–60	50–80	60–80	50–70	24–45	40–60	50–70	60–90	60–100	30–50
,, width (µm)	18–24	16–18	18–22	16–25	18–25	8–10	6–7	9–10	6–7	12–15	8–10	7–14	6–7
Ridges long	+	+	+	+	+	+	+	–	+	+	+	+	–
,, smooth	+	+, –	+	+, –	+, –	+	+	+	+	+	+	+	+
,, single	–	–	–	–	–	+	+	+	+	+	+	+	+
,, with many branches	–	–	–	–	–	–	–	+	–	+	+	–	–
Ridge units distinct	+	–	+, –	+, –	+	+	+	+	–	+	–	–	–
,, unit length (µm)	15–18	–	12–18	14–18	16–28	15–18	16–20	12–16	–	20–28	16–24	–	–
,, ,, width (µm)	9–12	–	10–12	10–12	10–12	8–10	6–7	8–12	–	12–15	8–10	–	–
Cross-ridge frequency	1	1	1	2	2	1	1	1	1	2	2	0	0
Inter-ridge pattern development	2	2	2	2	1	2	2	2	2	2	1	1	1
,, structure	1, (5)	1, (5)	2, 5	3, 5	2, 4, 5	1, (5)	1, (5)	2, 5	4, 5	2, (5)	1	1	2, 5
Rectangular unit length (µm)	45	45	21–30	20	30–40	36–40	40	31	–	30–35	35–45	40	18–24
,, ,, width (µm)	15	15	12–15	13	15–22	15–18	16	15	–	18–20	18–20	12	12–14
Oval unit diameter (µm)	20	20	18–20	18–20	20–22	20–25	16–20	20	17–20	24	–	–	18–21
Triangular unit dimension (µm)	–	–	–	–	20–22	–	–	–	17–20	–	–	–	–
Inter-ridge surface	1	1	1	1	1, 4, 5	1	1	1	2	(3), 4, 5	3, 4, 5	4	4
Unit surface texture	3	3, 2	3	2	1, 2	3	3	5	1	2	1, 2	1, 2	1
Wax development	0	0	1	0	1	0	0	0	0	0	0	0	0
Wax abundance	–	–	1	–	1	–	–	–	–	–	–	–	–
Wax structure	–	–	3	–	3	–	–	–	–	–	–	–	–
Sample Numbers	9, 10, 11	56, 57	41, 42, 43, 44	45, 46	36, 37, 38, 39, 40	1, 2, 3, 4, 5, 7, 8	50, 51, 52	47, 48, 49	93, 94, 97, 99, 102, 104	6	100, 101	111, 112, 113	98, 103 105

* For key to attributes see p. 92.

Group III: Patterns 27–30 (Table 4, Figs 10–11) form a group characterized by an undulate inter-ridge surface which is made up of 2–5 sets of predominantly triangular, oval or round units. Wax is usually absent.

TABLE 4

Seed surface structure of ridged *Zieria* seeds: Group III

Attribute* / Pattern No.	27	28	29	30
Ridge development	2	1	3	1
,, spacing (μm)	40–70	70–90	40–60	25–75
,, width (μm)	10–14	10–14	6–7	6–7
Ridges long	+	–	+	+
,, smooth	+	+	+	+
,, single	+	+	+	+
,, with many branches	–	+	+	+
Ridge units distinct	+	–	+, –	–
,, unit length (μm)	14–18	–	12–14	–
,, ,, width	10–14	–	6–7	–
Cross-ridge frequency	0	2	2	1
Inter-ridge pattern development	2	1	1	2
,, ,, structure	2, 4, 5	5	3, 5	4, 5
Rectangular unit length (μm)	30	–	16	–
,, ,, width (μm)	12	–	14	–
Oval unit diameter (μm)	15–20	20–30	15	21–24
Triangular unit dimension (μm)	14–18	–	–	12–18
Inter-ridge surface	3	3	3	3
Unit surface texture	4	1, 2	1, 2	1, 2
Wax development	0	0	0	0, 2
Wax abundance	–	–	–	1
Wax structure	–	–	–	3
Sample Numbers	95, 96	106, 107, 108	53, 54, 55	76, 79

* For key to attributes see p. 92.

Patterns 31–38 (Table 5, Figs 11–13) appear to be very distinct; they cannot be readily assigned to any of the groups described above.

Non-ridged surface patterns

Two of the 40 patterns are unridged. Pattern 39 (Fig. 13E, F) is colliculate with parallel rows of rectangular units (30–38 x 15–20 μm) and oval units (22–24 μm across) giving a ribbed appearance; the surface texture of the units is coarsely scabrate-striate. Pattern 40 is tuberculate; the tubercles are c. 20 μm high, 18–25 μm in diameter and smooth-surfaced with areas between the tubercles also smooth below crystalline wax.

The colliculate-ribbed pattern is unique in *Zieria* and has not yet been found in other genera of the tribe Boronieae (40 samples in 15 genera, Powell unpublished data).

Tuberculate patterns are found in some other members of the tribe Boronieae, for example, in *Boronia coerulescens*, *B. ledifolia* and *Geleznowia verrucosa* (Powell, unpublished data).

Taxonomic significance of seed morphology

In order to assess the taxonomic significance of seed-morphology in this genus, the seed surface data are compared in Table 6 with the taxa defined by Armstrong (unpubl.).

TABLE 5

Seed surface structure of ridged *Zieria* seeds: very distinct patterns

Attribute* / Pattern No.	31	32	33	34	35	36	37	38
Ridge development	1	1	3	1	1	2	2	3
,, spacing (μm) ..	55–80	25–40	18–20	40–60	45–60	40–50	20–26	23–35
,, width (μm)	12–14	9–12	15–20	10–17	10–12	7–14	15–18	20–30
Ridges long	–	–	+	+	+	+	+	+
Ridges smooth	+	–	+	–	+	+	+	–
,, single	+	+	–	+	+	+	+	–
,, with many branches	+	+	+	+	–	–	–	–
Ridge units distinct ..	–	–	+	+	–	–	+	+
,, unit length (μm) ..	–	–	12–15	16–20	–	–	10–12	14–17
,, ,, width (μm) ..	–	–	7–9	10–17	–	–	14–18	11–14
Cross-ridge frequency ..	1	0	2	1	0	1	0	1
Inter-ridge pattern development ..	1	1	1	2	2	2	1	1
,, structure ..	1, 4	2, 4	2	2, 4, 5	3, 5	3	3, 4	3
Rectangular unit length (μm)	35–45	25–30	10–12	25	20–25	20	20–24	25
,, ,, width (μm)	16–24	12–15	8–10	16	18–20	16–20	10–12	21
Oval unit diameter (μm) ..	–	–	–	20	12–15	–	–	–
Triangular unit dimensions (μm)	20	20–25	–	20–22	–	–	12–16	–
Inter-ridge surface.. ..	3, 4	3	3, 4	2	2	3	6	1
Unit surface texture ..	1	6	2	4	4	1	1	1
Wax development ..	0	0	0	0	2	2	2	2
Wax abundance ..	–	–	–	–	3	1, 2	1	3
Wax structure	–	–	–	–	4	2	2	1
Sample Numbers	110	119	92	83, 84	85	13, 14	28	114, 115, 116, 117, 118

* For key to attributes see p. 92.

TABLE 6

Zieria taxa compared with seed patterns and groups

Taxon		Seed pattern: Group	Seed pattern: Number	Seed sample numbers
Z. arborescens	ssp. "*a*" ..	II B	19	1, 2, 3, 4, 5, 7, 8
		II C	23	6
Z. aspalathoides	ssp. "*a*" ..	I B	6	12, 15, 16, 18, 19
		**	36	13, 14
		I C	10	17
	ssp. "*b*" ..	I B	9	20, 21, 22
	ssp. "*c*" ..	I B	6	23, 24
Z. chevalieri	..	I B	4	29
Z. cytisoides	ssp. "*a*" ..	II A	18	36, 37, 38, 39, 40
	ssp. "*b*" ..	II A	16	41, 42, 43, 44
Z. fraseri	ssp. "*a*" ..	I A	1	63
	ssp. "*b*" ..	I B	5	30, 31, 32, 34, 35
		I A	3	33

TABLE 6—*continued*

Taxon		Seed pattern		Seed sample numbers
		Group	Number	
Z. furfuracea	ssp. "*a*" ..	II A	17	45, 46
	ssp. "*b*" ..	II B	21	47, 48, 49
Z. granulata		II B	20	50, 51, 52
Z. involucrata		II A	15	56, 57
Z. laevigata	ssp. "*a*" ..	I A	2	58, 59, 60, 61, 62
	ssp. "*b*" ..	I B	8	65, 66, 67, 70, 71, 72, 73, 74, 75
		I C	11	68, 69
Z. minutiflora	ssp. "*a*" ..	I C	13	77, 78, 80, 81
		III	30	76, 79
	ssp. "*b*" ..	I C	13	82
Z. murphyi		**	34	83, 84
Z. obcordata	ssp. "*a*" ..	**	35	85
Z. pilosa		**	40	86, 87, 88, 89, 90, 91
Z. robusta		**	33	92
Z. smithii	ssp. "*a*" ..	II B	22	93, 94, 97, 99, 102, 104
		II C	24	100, 101
		II D	26	98, 103
		III	27	95, 96
	ssp. "*b*"	III	28	106, 107, 108
		II D	26	105
		**	39	109
Z. sp. nov. '*A*'		I C	12	25, 26, 27
Z. sp. nov. '*B*'		**	37	28
Z. sp. nov. '*C*'		III	29	53, 54, 55
Z. sp. nov. '*D*'		I B	7	64
Z. sp. nov. '*E*'	ssp. "*a*" ..	**	31	110
	ssp. "*b*" ..	II D	25	111
	ssp. "*c*" ..	II D	25	112, 113
Z. sp. nov. '*F*'		II A	14	9, 10, 11
Z. sp. nov. '*G*'		**	32	119
Z. veronicea		**	38	114, 115, 116, 117, 118

** Very distinct pattern (see Table 5).

In general, seed surface morphology is taxonomically useful. Amongst the better-sampled taxa the surface pattern is constant within *Z. aspalathoides* ssp. '*b*', *Z. cytisoides* ssp. '*a*' and ssp. '*b*', *Z. furfuracea* ssp. '*b*', *Z. granulata*, *Z. laevigata* ssp. '*a*', *Z. pilosa*, *Z.* sp. nov. '*A*', *Z.* sp. nov. '*C*', *Z.* sp. nov. '*F*' and *Z. veronicea*. Amongst the less well-sampled taxa the surface pattern of *Z. fraseri* ssp. '*a*', *Z. furfuracea* ssp. '*a*', *Z. involucrata*, *Z. murphyi*, *Z. obcordata* ssp. '*a*', *Z. robusta*, *Z.* sp. nov. '*B*', *Z.* sp. nov. '*E*' ssp. '*a*' and *Z.* sp. nov. '*G*' is distinct and seems likely to remain constant with further sampling.

In *Z. chevalieri* and *Z.* sp. nov. '*D*' the distinctiveness of the pattern may be lost with further sampling, falling within the range of variation shown in *Z. fraseri* ssp. '*b*' and *Z. laevigata* ssp. '*b*' respectively, and in the case of *Z. minutiflora* ssp. '*b*', *Z. aspalathoides* ssp. '*c*' and *Z.* sp. nov. '*E*' ssp. '*b*' the surface pattern is shared with other taxa of each species.

In 7 taxa (Table 6) more than one seed-type per taxon occurs: *Z. arborescens* ssp. '*a*', *Z. minutiflora* ssp. '*a*', *Z. fraseri* ssp. '*b*' and *Z. laevigata* ssp. '*b*' each have two types of pattern, *Z. aspalathoides* ssp. '*a*' and *Z. smithii* ssp. '*b*' have three types and *Z. smithii* ssp. '*a*' has four types. In such cases seed surface morphology does not correlate well with the taxonomy. Considering these taxa and their surface patterns in more detail:

(1) *Z. arborescens*: Two seed surface patterns are present within ssp. '*a*' (Table 6; Figs. 8E, F; 9E, F). Pattern 19 is predominant, being found in 7 out of 8 samples. It differs from 23 in the frequency of branches and cross-ridges, in ridge unit dimensions, in inter-ridge surface pattern and somewhat in width and spacing of ridges and the dimensions of the inter-ridge units.

The patterns are not very similar. The predominance of 19 suggests that it is the characteristic pattern of *Z. arborescens* ssp. '*a*' and 23 can be considered as a relatively rare deviant. Pattern 19 is similar to pattern 20 (found in *Z. granulata*) and 21 (*Z. furfuracea* ssp. '*b*') whilst pattern 23 is structurally very similar to 24 (found in *Z. smithii* ssp. '*a*').

(2) *Z. aspalathoides*: Four seed surface patterns are present (Table 6; Figs. 5C, D; 6A, B; C, D; 12G, H). Pattern 6 is the commonest being found in 7 out of 13 samples. All four patterns have long ridges, smooth-surfaced ridges and inter-ridge units, and persistent wax. Pattern 36 differs from all others in having narrow ridges and an undulate inter-ridge surface. Patterns 6, 9 and 10 are similar, differing one from another only to a small extent in width of ridges and distinctness and structure of the inter-ridge pattern.

The seed data support the taxonomic recognition of ssp. '*b*' since seed pattern 9 is restricted to this taxon, but do not reflect the taxonomic recognition of ssp. '*c*' since pattern 6 is present also in ssp. '*a*'. The distinctiveness of pattern 36 suggests that ssp. '*a*' is heterogeneous but this is not indicated by other morphological data.

(3) *Z. fraseri*: Three seed surface patterns (1, 3, and 5) are present (Table 6; Figs. 4A, B; E, F; 5A, B). All have long, relatively broad, smooth-surfaced double ridges, a ribbed inter-ridge surface and persistent wax. They differ, one from another, in the frequency of cross-ridges, the dimensions of the inter-ridge units, in wax structure and somewhat in the spacing of ridges, in ridge unit dimensions, in frequency of branches and in surface texture of inter-ridge units.

The seed surface data reflect the taxonomic recognition of *Z. fraseri* ssp. '*a*' but suggest that *Z. fraseri* ssp. '*b*' is heterogeneous for this character. Pattern 5, the predominant pattern of this subspecies, resembles more closely patterns 4 (found in the New Caledonia species, *Z. chevalieri*) and 6 (found in *Z. aspalathoides* ssp. '*a*' and ssp. '*c*') than pattern 3.

(4) *Z. laevigata*: Three seed surface patterns (2, 8, and 11) are present (Table 6; Figs. 4C, D; 5G, H; 6E, F). The patterns are similar in having double, generally smooth-surfaced ridges with few branches, distinct ridge units, smooth inter-ridge units and persistent wax. Both pattern 8 and 11 differ from 2 in ridge development, ridge length, cross-ridge frequency and abundance of wax; from each other they differ in inter-ridge pattern structure.

The seed data and taxonomy are very strongly correlated in *Z. laevigata* ssp. '*a*' since seed pattern 2 (well represented by 5 seed samples) is restricted to this taxon. *Z. laevigata* ssp. '*b*', on the other hand, is heterogeneous in seed surface morphology, comprising patterns 8 and 11. Pattern 8 is predominant; pattern 11 may be considered as a less common deviant, the inter-ridge structure being undeveloped in this case.

The close taxonomic relationship between ssp. '*a*' and ssp. '*b*' is not apparent from the seed data. Pattern 2 more closely resembles 3 (*Z. fraseri* ssp. '*b*') whereas patterns 8 and 11 are more similar to 7 (*Z.* sp. nov. '*D*').

(5) *Z. minutiflora*: Two seed surface patterns (13, 30) are present (Table 6; Figs. 7A, B; 12A, B). Both types have long, smooth ridges with few cross-ridges, a distinct inter-ridge pattern comprising mainly oval and triangular-shaped units and an undulate inter-ridge surface. Pattern 13 is predominant being present in 5 of the 7 seed samples studied. It is quite distinct from pattern 30 in having broad, double ridges which are prominent and erect, distinct ridge units and inter-ridge units of different dimensions.

There is no agreement between the seed data and the taxonomic data for this species. Seed pattern 13 is present in both subspecies and the concurrence of patterns 13 and 30 within ssp. '*a*' indicate it is heterogeneous for this character.

(6) *Z. smithii*: Six seed surface patterns are present (Table 6; Figs. 9C, D; 9G, H; 10 C–H; 13E, F). Pattern 22 is common, being found in 6 of the 17 specimens sampled in this taxon. Patterns 26 and 28 are each found in three samples, 24 and 27 in two samples and 39 is recorded from a single sample. All types have single, smooth-surfaced ridges and lack wax. In some cases the ridges are narrow or very narrow but relatively widely-spaced across the seed, and ridge units are indistinct. The types differ in almost every other attribute: ridges may be long or short, branches and cross-ridges few or many, the inter-ridge pattern distinct or indistinct. Pattern units differ as do inter-ridge surfaces and unit surface texture.

The seed data do not coincide at all with the taxonomic data: in both subspecies seed morphology is heterogeneous. In ssp. '*a*' there are 4 seed surface patterns. Patterns 22, 24 and 26 all fall within Group II seed type but are not closely associated: 22 (subgroup B) shows some similarity to 19, 20, and 21 (found in *Z. arborescens* ssp. '*a*', *Z. granulata* and *Z. furfuracea* ssp. '*b*' respectively) while patterns 24 (subgroup C) and 26 (subgroup D) resemble more closely patterns 23 and 25, found in *Z. arborescens* ssp. '*a*' and *Z.* sp. nov. '*E*' ssp. '*b*' and '*c*' respectively. Pattern 27 is in Group III seed type and is loosely associated there with patterns 28, 29 and 30, found in *Z. smithii* ssp. '*b*', *Z.* sp. nov. '*C*' and *Z. minutiflora* ssp. '*a*' respectively.

In ssp. '*b*' three surface patterns occur. One of these (26) is recorded already in ssp. '*a*' and another (39) is very distinct, being non-ridged in structure. The third pattern (28) predominates, being found in 3 out of 5 samples; it resembles more closely pattern 29 (*Z.* sp. nov. '*C*') than others recorded in *Z. smithii*.

The taxonomic recognition of the two *Z. smithii* subspecies is not reflected by the extremely diverse seed surface patterns. Although *Z. smithii* has an extensive distribution pattern (Atherton, N. Queensland to E. Gippsland, Victoria) there is no correspondence between seed pattern variation and phytogeography.

Sources of Variation

Since almost all of the material used came from herbarium sheets it seems likely that some of the variation present in well-sampled taxa (e.g. *Z. laevigata*, *Z. smithii*) could be related to differential treatment (drying and storing) following field collection, and some to the maturity of the seeds studied. Although all samples selected were assigned to either mature (dark coloured, plump seeds) or immature (lighter coloured, flat seeds), the actual maturity of the former group may have varied: the genus has an explosive seed dispersal mechanism and hence any apparently mature seeds remaining inside capsules on herbarium sheets may, in fact, be somewhat immature.

Developmental studies of material grown under controlled conditions may help also to explain some of the variation; they would give information on internal as well as surface structure and provide a better base for discussion of intra-specific variation and relationships.

Newell and Hymowitz (1978) have recently studied seed coat variation in *Glycine* subgenus *Glycine* using fresh seed from greenhouse grown plants. They examined 4–20 seeds per accession and a number of accessions per species. They found that there was very little variability within accessions but the variation was often considerable between accessions within species.

Relationships of Taxa

It has been possible to establish certain groups of seed surface patterns on the basis of structural similarities (Tables 2–5) and these are listed in Table 6 alongside the taxonomic entities.

In some cases the close relationship of taxa indicated morphologically is supported by the seed surface data, for example, general morphology suggests a close relationship between *Z. chevalieri*, *Z. fraseri*, *Z. laevigata* and *Z.* sp. nov. '*D*', and this relationship is supported by the seed surface data (seed pattern 4 (*Z. chevalieri*) is similar to pattern 5 (*Z. fraseri*); patterns 1 and 3 (*Z. fraseri*) are similar to pattern 2 (*Z. laevigata*) whilst pattern 8 (*Z. laevigata*) is very similar to pattern 7 (*Z.* sp. nov. '*D*')). Seed surface data coincides with the general morphological similarities between *Z. aspalathoides* (pattern 10), *Z.* sp. nov. '*A*' (pattern 12) and *Z. minutiflora* (pattern 13) and this concurrence is also seen in the three closely related species *Z. arborescens* (patterns 21 and 26), *Z. smithii* (patterns 24, 27 and 29) and *Z.* sp. nov. '*E*' (pattern 28). Again, the close relationship between *Z. cytisoides*, *Z. involucrata*, and *Z.* sp. nov. '*F*' indicated by general morphology, is supported by the seed surface data: seed pattern 18 (*Z. involucrata*) is similar to 19 (*Z. cytisoides*) and pattern 17 (*Z.* sp. nov. '*F*') is similar to both these patterns.

In other cases possible relationships indicated by the seed surface data are not correlated with general morphological data, for example: *Z. arborescens* (pattern 19) is not morphologically similar to either *Z. granulata* (pattern 20) or to *Z. furfuracea* ssp. '*b*' (pattern 21), *Z. furfuracea* ssp. '*a*' (pattern 17) is not similar to *Z. cytisoides* (patterns 16, 18) or to *Z. involucrata* (pattern 15); *Z. laevigata* (pattern 11) does not resemble closely either *Z. minutiflora* (pattern 13) or *Z.* sp. nov. '*A*' (pattern 12), and *Z. smithii* (patterns 27, 28) is not morphologically similar to either *Z.* sp. nov. '*C*' (pattern 29) or to *Z. minutiflora* (pattern 13). In these cases similarity in seed surface structure may be explained in terms of parallel evolution.

CONCLUSIONS

The detailed survey of seed surface patterns in *Zieria* indicates that there is a wide range of seed-morphological variation in the genus. While there is considerable coincidence between the seed data and the taxonomic entities recognized on other grounds, it is by no means universal. Hence seed morphology is of use for distinguishing taxa in only some instances within this genus. Also, as a basis for indicating phylogenetic relationship the seed data appear to be helpful occasionally in *Zieria* but conclusions must, in general, be based on other data. These findings contrast with many other studies where seed surface data have provided a strong base for delimitation of taxonomic entities and for phylogenetic conclusions.

Many earlier SEM studies have made use of only a single sample of seeds per taxon and hence some of the exact correlations between surface structure and taxonomic entities which have been reported may be more apparent than real. The present study indicates the necessity of sampling a taxon as widely as possible so that the amount of variation present both within and between taxa can be elucidated.

In *Zieria*, it may be concluded that for those taxa with diverse seed structure, evolution in seed surface patterns may be proceeding at a relatively rapid rate compared with other morphological features.

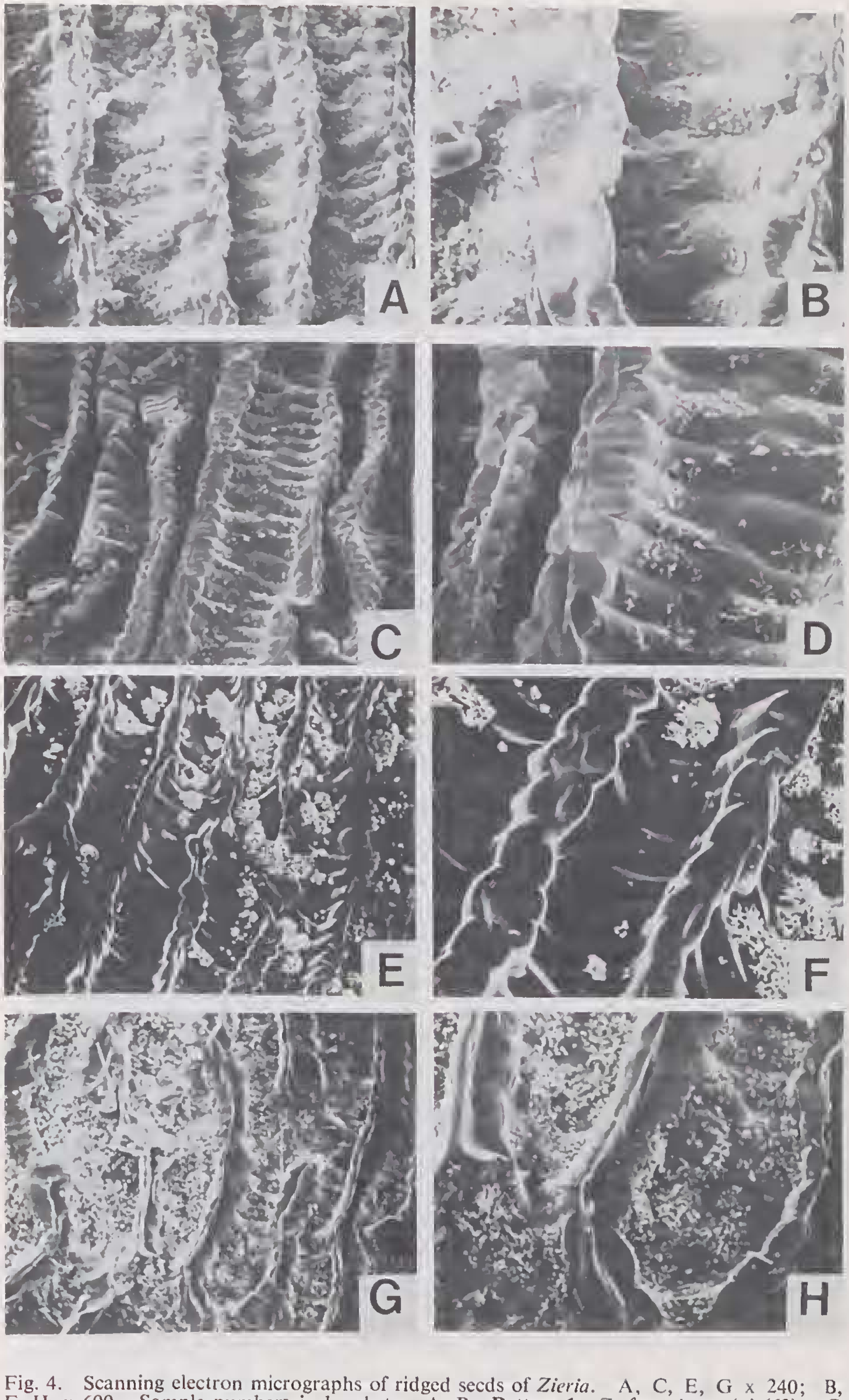

Fig. 4. Scanning electron micrographs of ridged seeds of *Zieria*. A, C, E, G x 240; B, D, F, H, x 600. Sample numbers in brackets. A, B; **Pattern 1:** *Z. fraseri* ssp. '*a*' (63). C, D; **Pattern 2:** *Z. laevigata* ssp. '*a*' (61). E, F; **Pattern 3:** *Z. fraseri* ssp. '*b*' (33). G, H; **Pattern 4:** *Z. chevalieri* (29).

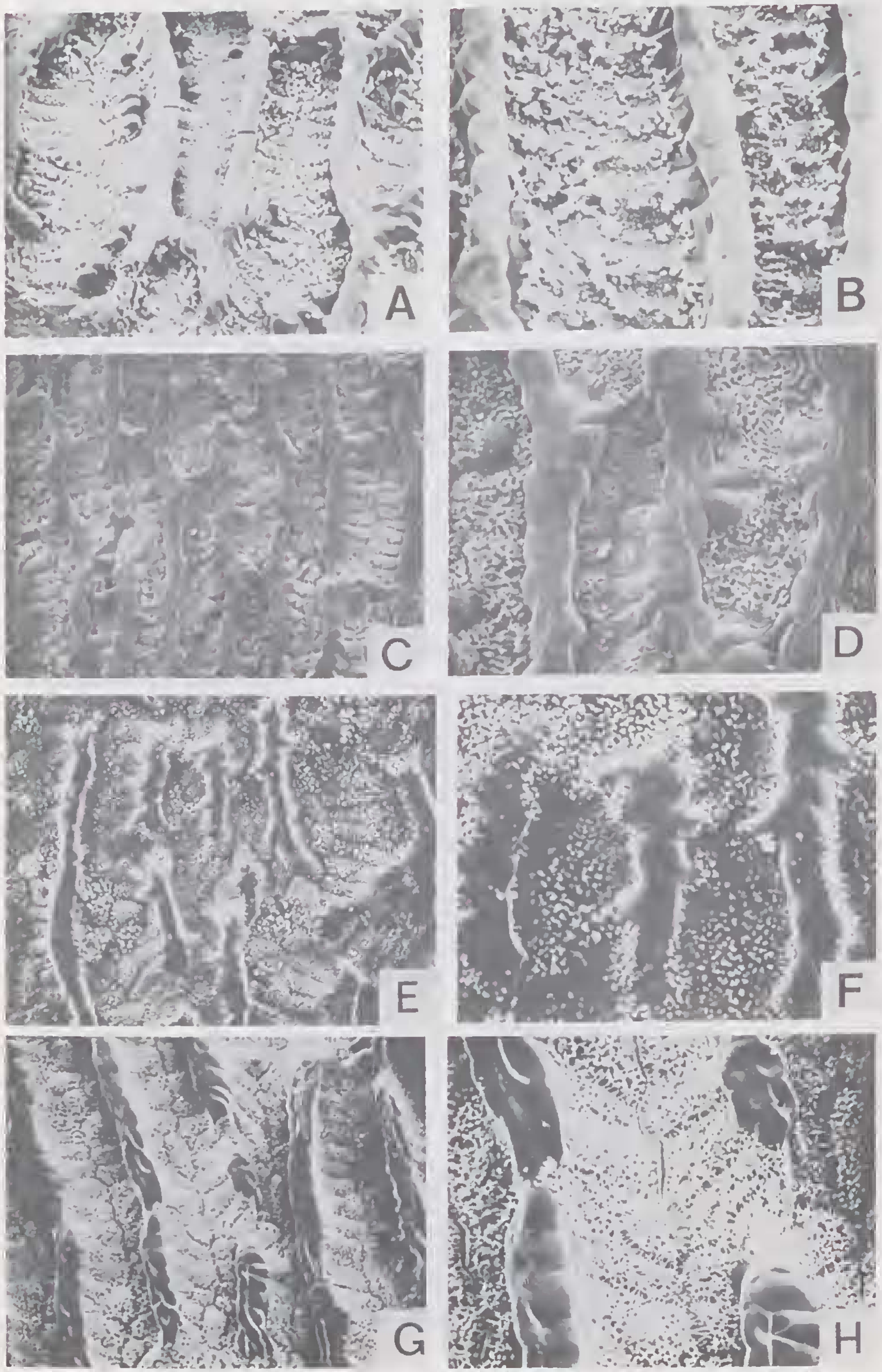

Fig. 5. Scanning electron micrographs of ridged seeds of *Zieria*. A, C, E, G x 240; B, D, F, H x 600. Sample numbers in brackets. A, B; **Pattern 5:** *Z. fraseri* ssp. '*b*' (35). C, D; **Pattern 6:** *Z. aspalathoides* ssp. '*a*' (16). E, F; **Pattern 7:** *Z.* sp. nov. '*D*' (64). G, H; **Pattern 8:** *Z. laevigata* ssp. '*b*' (73).

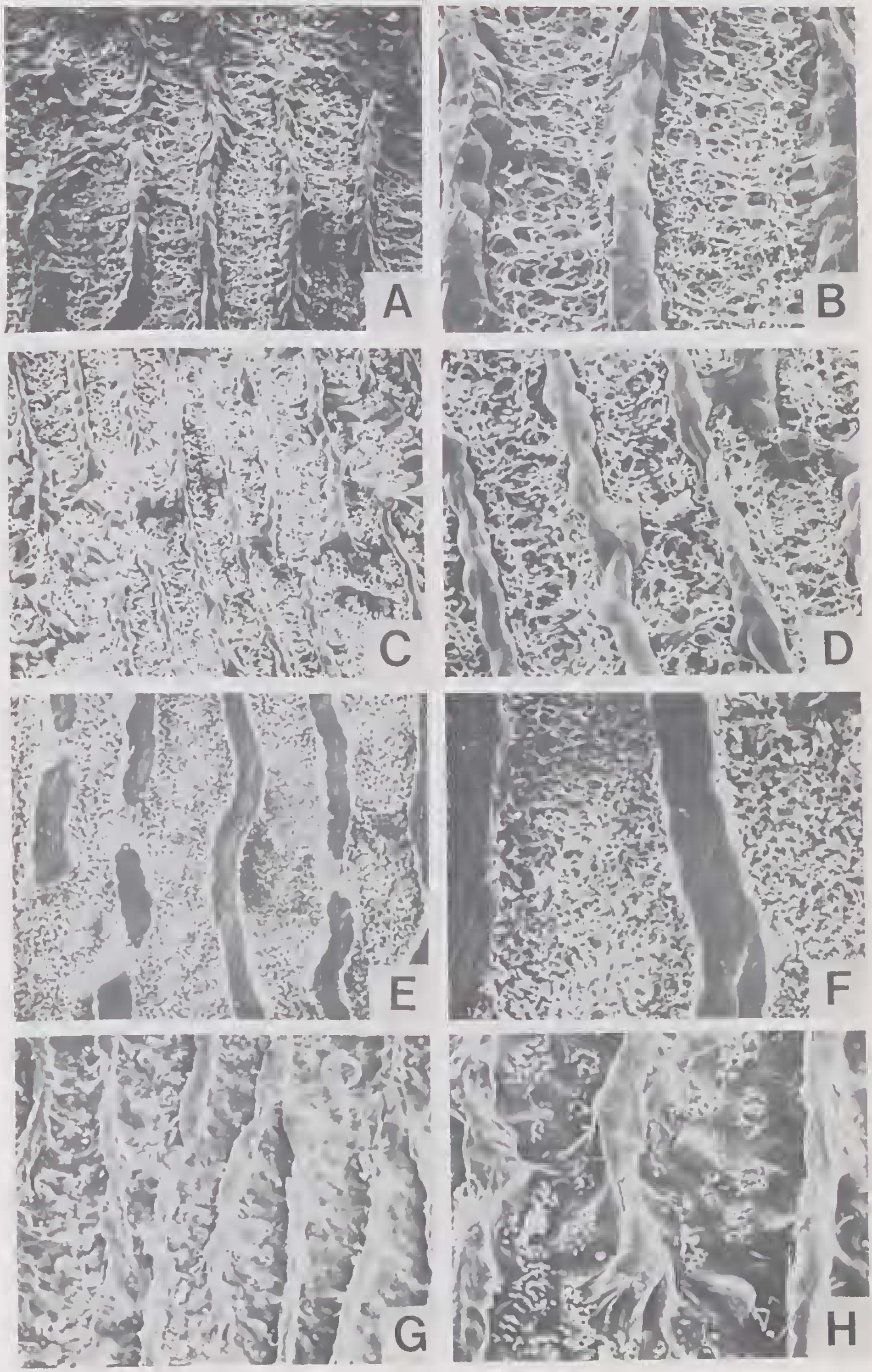

Fig. 6. Scanning electron micrographs of ridged seeds of *Zieria*. A, C, E, G x 240; B, D, F. H x 600. Sample numbers in brackets. A, B; **Pattern 9:** *Z. aspalathoides* ssp. '*b*' (21). C, D; **Pattern 10:** *Z. aspalathoides* ssp. '*a*' (17). E, F; **Pattern 11:** *Z. laevigata* ssp. '*b*' (68). G, H; **Pattern 12:** *Z.* sp. nov. '*A*' (26).

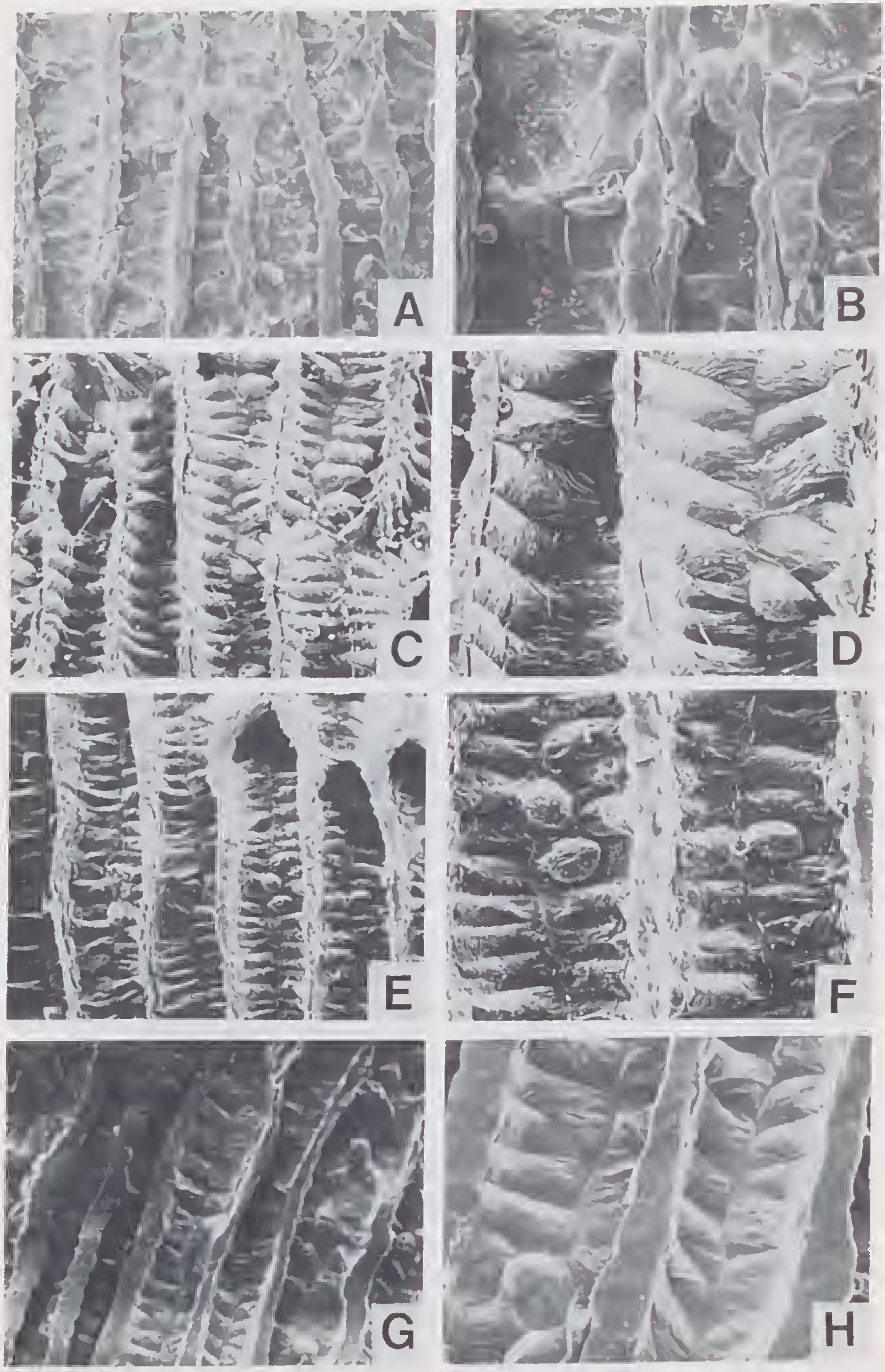

Fig. 7. Scanning electron micrographs of ridged seeds of *Zieria*. A, C, E, G x 240; B, D, F, H x 600. Sample numbers in brackets. A, B; **Pattern 13:** *Z. minutiflora* ssp. '*b*' (82). C, D; **Pattern 14:** *Z.* sp. nov. '*F*' (9). E, F; **Pattern 15:** *Z. involucrata* (56). G, H; **Pattern 16:** *Z. cytisoides* ssp. '*b*' (43).

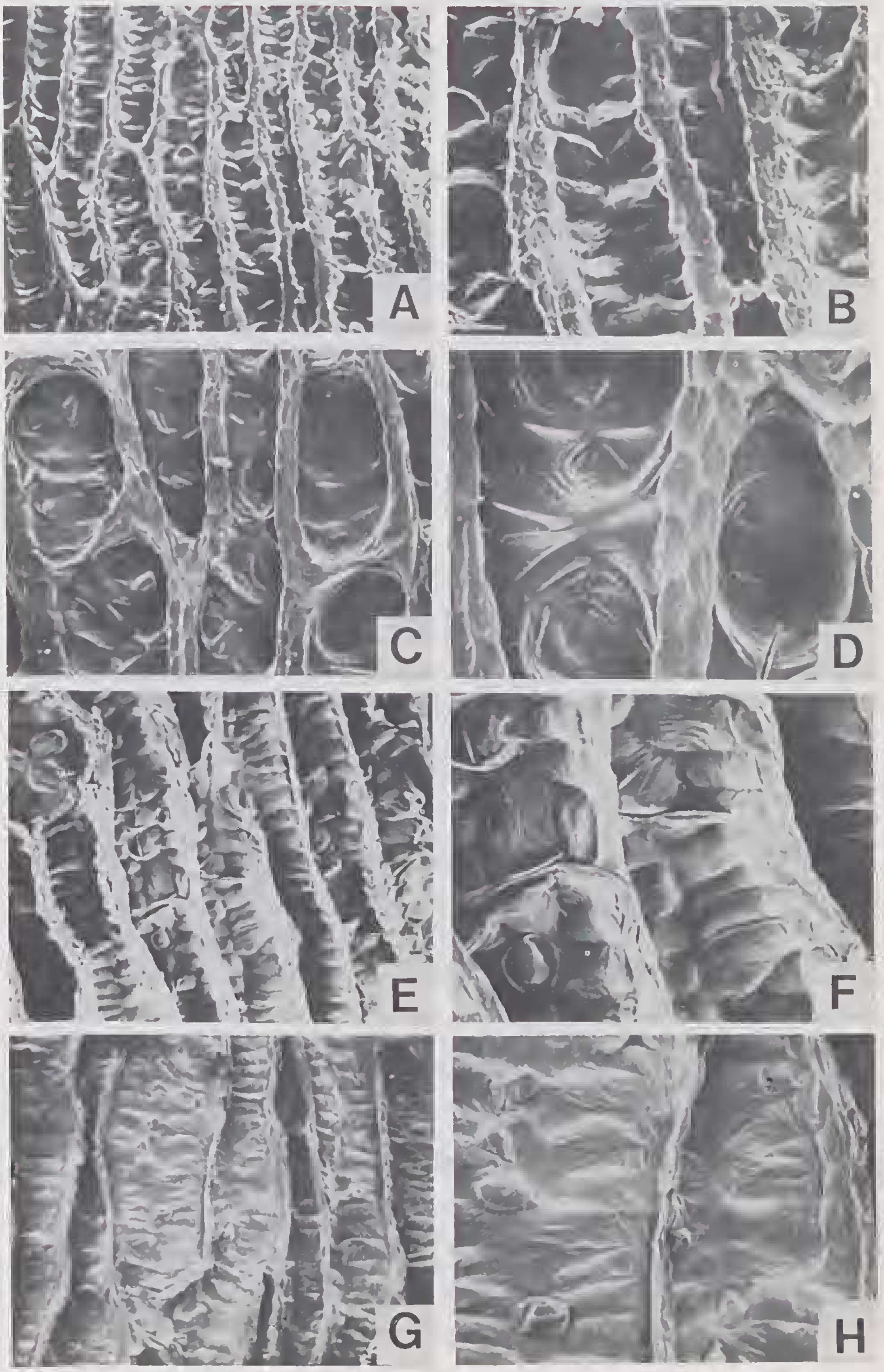

Fig. 8. Scanning electron micrographs of ridged seeds of *Zieria*. A, C, E, G x 240; B, D, F, H x 600. Sample numbers in brackets. A, B; **Pattern 17:** *Z. furfuracea* ssp. '*a*' (46). C, D; **Pattern 18:** *Z. cytisoides* ssp. '*a*' (37). E, F; **Pattern 19:** *Z. arborescens* ssp. '*a*' (3). G, H; **Pattern 20:** *Z. granulata* (51).

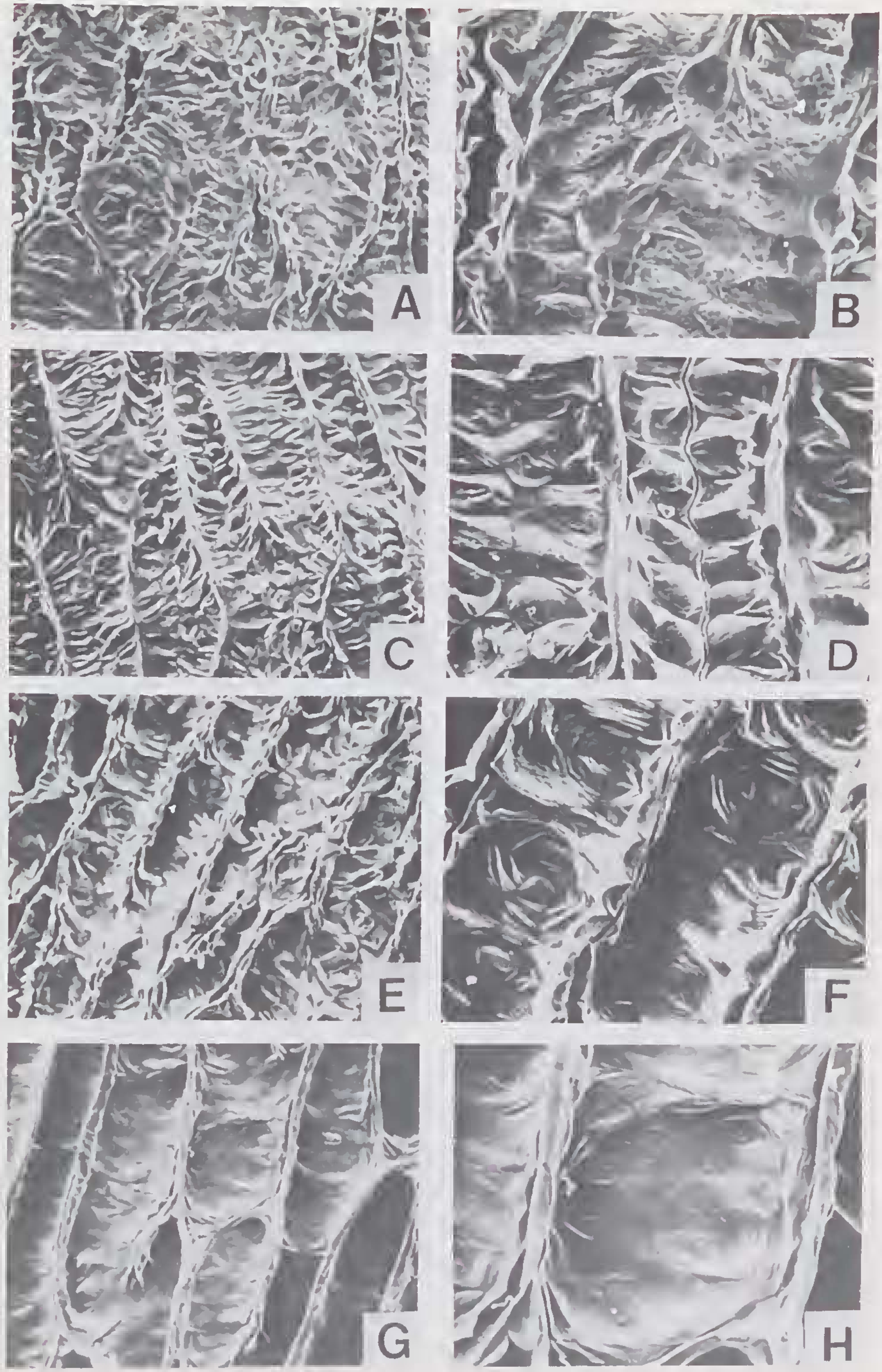

Fig. 9. Scanning electron micrographs of ridged seeds of *Zieria*. A, C, E, G x 240; B, D, F, H x 600. Sample numbers in brackets. A, B; **Pattern 21:** *Z. furfuracea* spp. '*b*' (49). C, D; **Pattern 22:** *Z. smithii* ssp. '*a*' (102). E, F; **Pattern 23:** *Z. arborescens* ssp. '*a*' (6). G, H; **Pattern 24:** *Z. smithii* ssp. '*a*' (100).

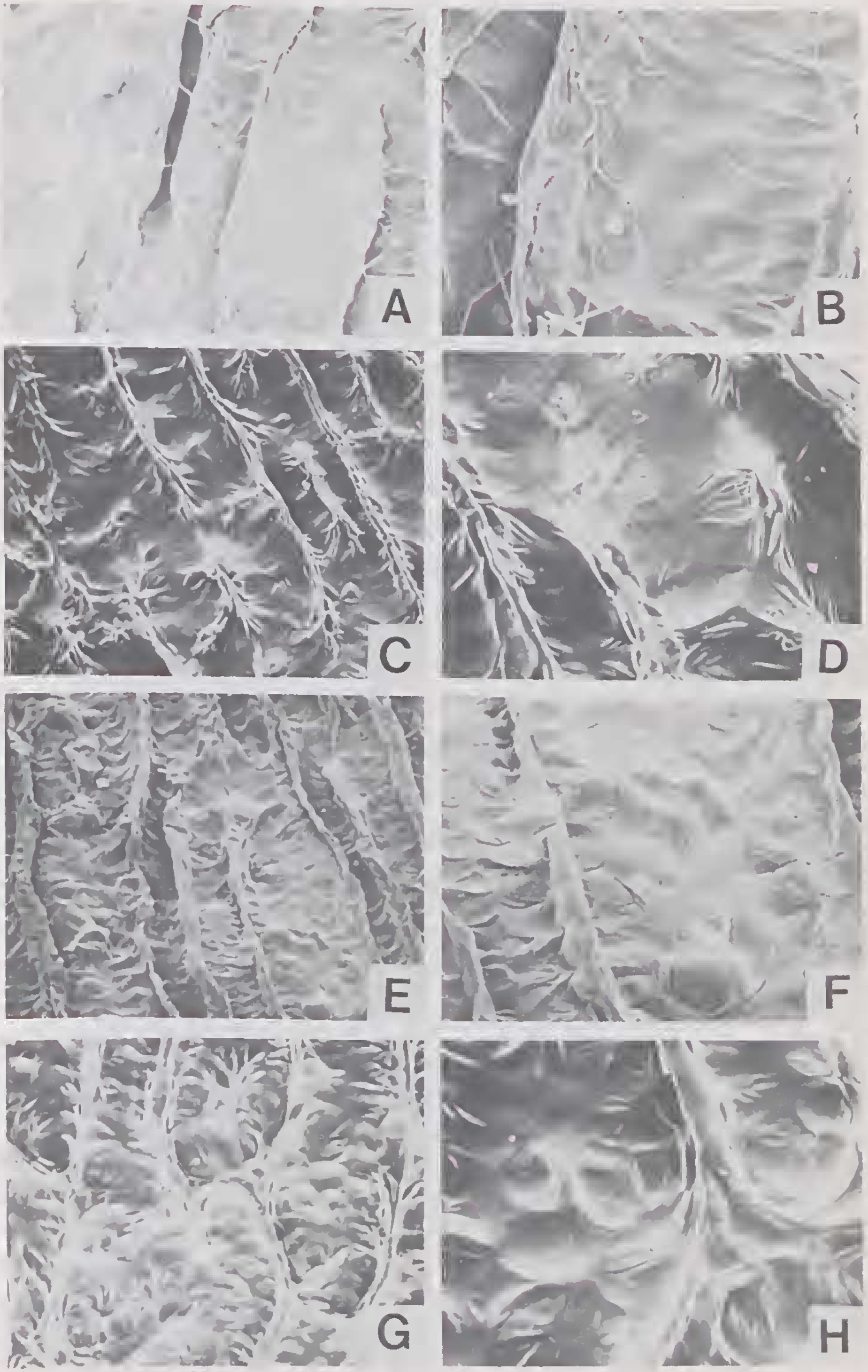

Fig. 10. Scanning electron micrographs of ridged seeds of *Zieria*. A, C, E, G x 240; B, D, F, H x 600. Sample numbers in brackets. A, B; **Pattern 25:** *Z.* sp. nov. '*E*' ssp. '*b*' (111). C, D; **Pattern 26:** *Z. smithii* ssp. '*a*' (103). E, F; **Pattern 27:** *Z. smithii* ssp. '*a*' (95). G, H; **Pattern 28:** *Z. smithii* ssp. '*b*' (106).

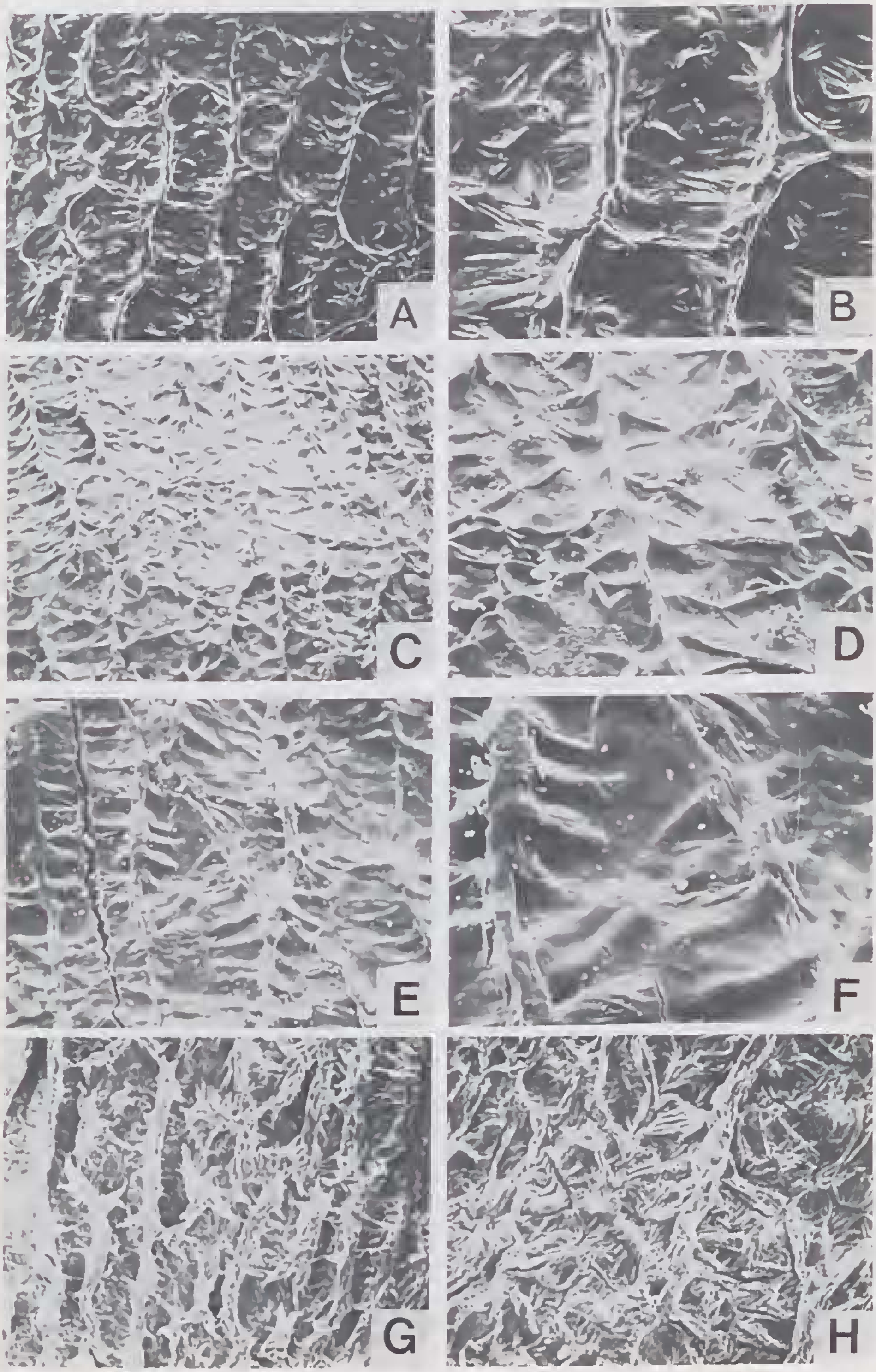

Fig. 11. Scanning electron micrographs of ridged seeds of *Zieria*. A, C, E, G x 240; B, D, F, H x 600. Sample numbers in brackets. A, B; **Pattern 29:** *Z*. sp. nov. '*C*' (55). C, D; **Pattern 30:** *Z. minutiflora* ssp. '*a*' (76). E, F; **Pattern 31:** *Z*. sp. nov. '*E*' ssp. '*a*' (76). G, H; **Pattern 32:** *Z*. sp. nov. '*G*' (119).

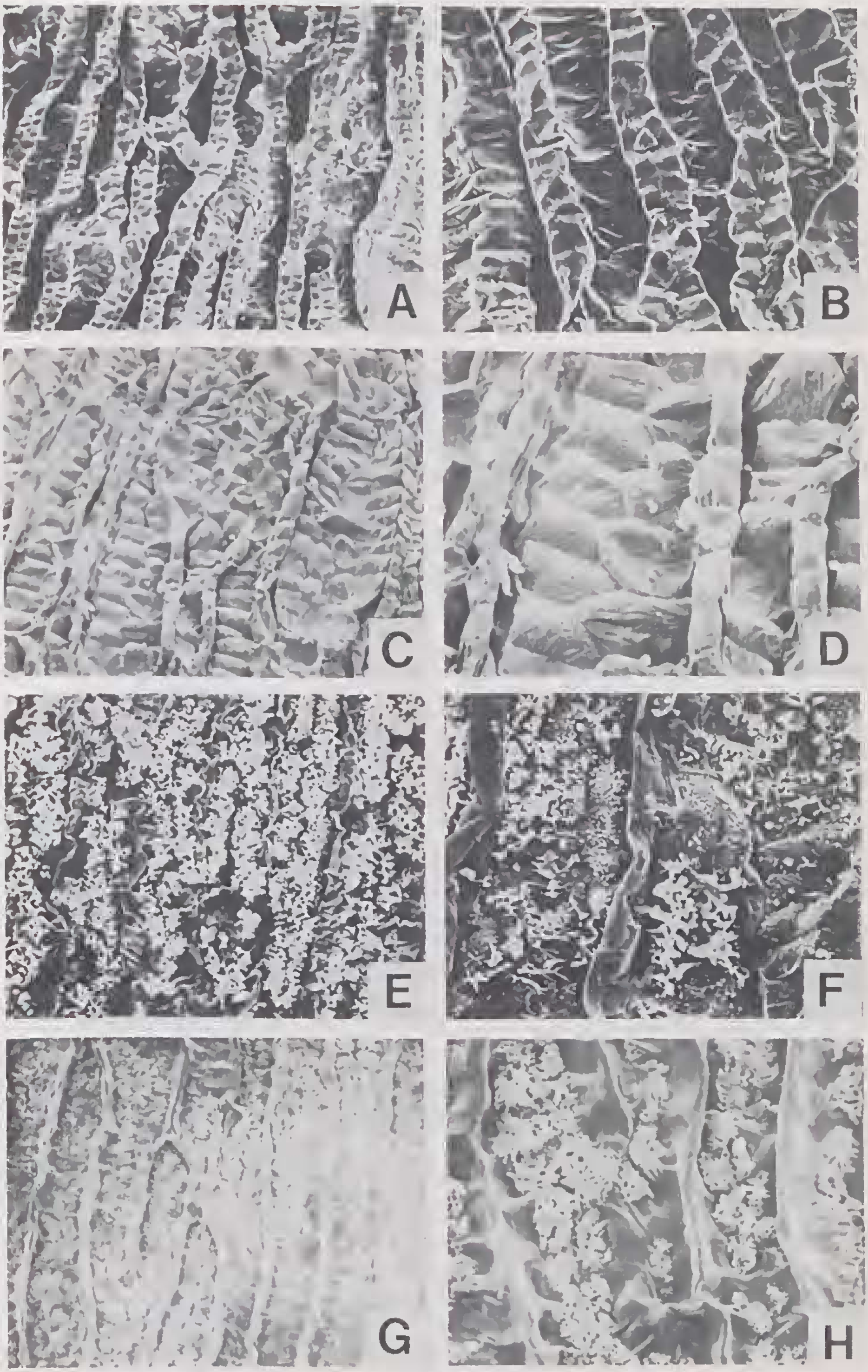

Fig. 12. Scanning electron micrographs of ridged seeds of *Zieria*. A, C, E, G x 240; B, D, F, H x 600. Sample numbers in brackets. A, B; **Pattern 33:** *Z. robusta* (92). C D; **Pattern 34:** *Z. murphyi* (84). E, F; **Pattern 35:** *Z. obcordata* (85). G, H; **Pattern 36:** *Z. aspalathoides* ssp. '*a*' (14).

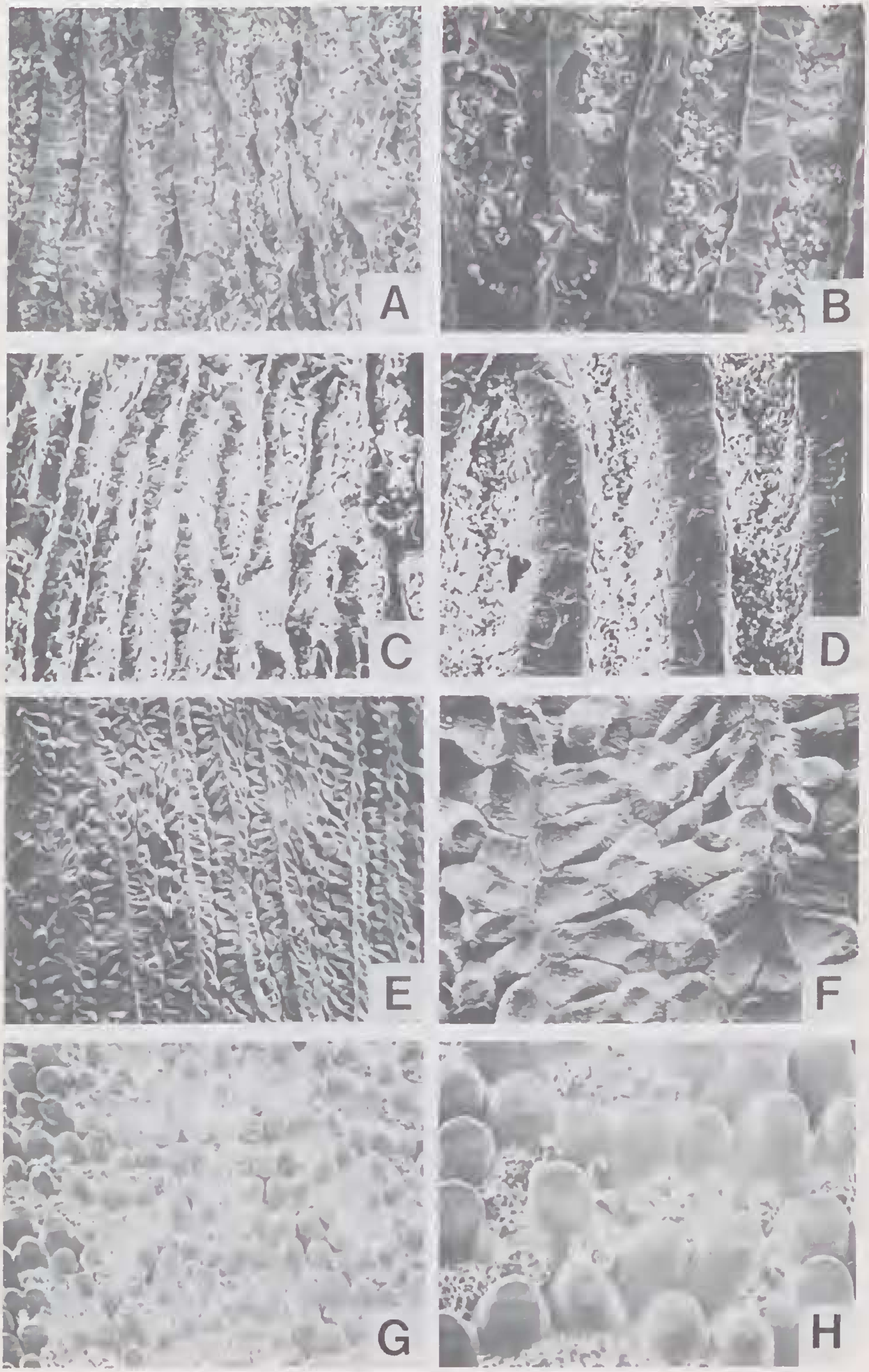

Fig. 13. Scanning electron micrographs of *Zieria*. A, C, E, G x 240; B, D, F, H x 600. Sample numbers in brackets. A, B; **Pattern 37:** *Z*. sp. nov. '*B*' (28). C, D; **Pattern 38:** *Z. veronicea* (118). E, F; **Pattern 39:** *Z. smithii* ssp. '*b*' (109). G, H; **Pattern 40:** *Z. pilosa* (86).

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REFERENCES

Bentham, G. (1863). 'Flora Australiensis.' Vol. 1, pp. 303–307. (Lovell Reeve: London.)

Blakely, W. F. (1941). Additions to the flora of New South Wales. *Austral. Naturalist* 10: 246.

Brisson, J. D. & Peterson, R. L. (1976). A critical review of the use of scanning electron microscopy in the study of the seed coat. *Illinois Inst. Tech. Res. Inst./SEM/1976*, 2: 477–495.

Chuang, T. I. & Heckard, L. R. (1972). Seed coat morphology in *Cordylanthus* (Scrophulariaceae) and its taxonomic significance. *Amer. J. Bot.* 59: 258–265.

Crow, G. E. (1979). The systematic significance of seed morphology in *Sagina* (Caryophyllaceae) under scanning electron microscopy. *Brittonia* 31: 52–63.

Domin, K. (1913). Seventh contribution to the flora of Australia. *Feddes Repert. Spec. Nov. Regni Veg.* 12: 132–133.

Echlin, P. (1968). The use of the scanning reflection electron microscope in the study of plant and microbial material. *J. Roy. Microscop. Soc.* 88: 407–418.

Engler, A. (1931). Rutaceae. In Engler, A. & Harms, H. 'Die Natürlichen Pflanzenfamilien.' Edn 2. Vol. 19a, pp. 187–358. (Engelmann: Leipzig.)

Engler, A. (revised Scholz, H.) (1964). Rutaceae. In A. Engler (Ed. H. Melchior), 'Syllabus der Pflanzenfamilien.' Edn 12. Vol. 2, pp. 263–266. (Gebrüder Borntraeger: Berlin.)

Forman, L. L. (1974). The endocarps of *Cocculus* (Menispermaceae). *Kew Bull.* 29: 477–481.

Godeau, M. (1973a). Etude au microscope électronique à balayage des téguments séminaux des *Arenaria* armoricains du groupe *serpyllifolia* L. *Compt. Rend. Hebd. Séances Acad. Sci.* 276D: 537–540.

Godeau, M. (1973b). Morphologie des graines des *Cochlearia* armoricains: Etude au microscope électronique à balayage. *Bull. Soc. Sci. Bretagne* 48: 229–239.

Heywood, V. H. (1969). Scanning electron microscopy in the study of plant materials. *Micron* 1: 1–14.

Heywood, V. H. (1971). The characteristics of the scanning electron microscope and their importance in biological studies. In Heywood, V. H. (Ed.). 'Scanning Electron Microscopy: Systematic and Evolutionary Applications.' pp. 1–16. (Academic Press: London.)

Hill, R. J. (1976). Taxonomic and phylogenetic significance of seed coat microsculpturing in *Mentzelia* (Loasaceae) in Wyoming and adjacent Western States. *Brittonia* 28: 86–112.

Huckerby, E., Marchant, R. & Oldfield, F. (1972). Identification of fossil seeds of *Erica* and *Calluna* by scanning electron microscopy. *New Phytol.* 71: 387–392.

Maiden, J. H. & Betche, E. (1911). Notes from the Botanic Gardens, Sydney. No. 16. *Proc. Linn. Soc. New South Wales* 35: 788–789.

Maiden, J. H. & Betche, E. (1916). 'A Census of New South Wales Plants.' pp. 114–115. (Govt. Printer: Sydney.)

Mueller, F. von (1875). 'Fragmenta Phytographiae Australiae.' Vol. 9, p. 116. (Govt. Printer: Melbourne.)

Murley, M. R. (1951). Seeds of the Cruciferae of Northeastern North America. *Amer. Midl. Naturalist* 46: 1–81.

Newell, C. A. & Hymowitz, T. (1978). Seed coat variation in *Glycine* Willd. subgenus *Glycine* (Leguminosae) by SEM. *Brittonia* 30: 76–88.

Schuyler, A. E. (1971). Scanning electron microscopy of achene epidermis in species of *Scirpus* (Cyperaceae) and related genera. *Proc. Acad. Nat. Sci. Philadelphia* 123: 29–52.

Seavey, S. R., Magill, R. E. & Raven, P. H. (1977a). Evolution of seed size, shape and surface architecture in the tribe Epilobieae (Onagraceae). *Ann. Missouri Bot. Gard.* 64: 18–47.

Seavey, S. R., Wright, P. & Raven, P. H. (1977b). A comparison of *Epilobium minutum* and *E. foliosum* (Onagraceae). *Madroño* 24: 7–12.

Skvortsov, A. K. & Rusanovitch, I. I. (1974). Scanning electron microscopy of the seed-coat surface in *Epilobium* species. *Bot. Not.* 127: 329–401.

Toivonen, H. & Timonen, T. (1976). Perigynium and achene epidermis in some species of *Carex* subg. *Vignea* (Cyperaceae) studied by scanning electron microscopy. *Ann. Bot. Fenn.* 13: 49–59.

Whiffin, T. & Tomb, A. S. (1972). The systematic significance of seed morphology in the neo-tropical capsular-fruited Melastomataceae. *Amer. J. Bot.* 59: 411–422.

White, C. T. (1932). Two previously undescribed Rutaceae from southeast Queensland. *Proc. Roy. Soc. Queensland* 43: 46–47.

White, C. T. (1942). Contributions to the Queensland flora. No. 7. *Proc. Roy. Soc. Queensland* 53: 208–210.

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